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OBSERVATIONS ON THE MALAGASY GENUS RHYNCHOPHORA (MALPIGHIACEAE)

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ABSTRACT. The Malagasy genera *Rhynchophora* Arènes and *Calyptostylis* Arènes are combined under the name *Rhynchophora*, and the new species *R. phillipsonii* W. R. Anderson is described and illustrated. It is morphologically androdioecious but probably functionally dioecious. The distribution of indehiscent fruits in the Malpighiaceae is discussed, with comments on the anomaly of multiseeded indehiscent fruits.

Rhynchophora Arènes, Notul. Syst. (Paris) 12: 127. 1946.—TYPE: *Rhynchophora humbertii* Arènes.

Calyptostylis Arènes, Notul. Syst. (Paris) 12: 131. 1946.—TYPE: *Calyptostylis humbertii* Arènes.

When Arènes described the two monotypic Malagasy genera *Rhynchophora* and *Calyptostylis*, he had mature fruits of the former and only very immature fruits of the latter. He distinguished the two genera on the basis of the fruits, saying that *Rhynchophora* has horizontal wings, one per carpel, at the middle of the indehiscent fruit, while he described the enlarging ovary of *Calyptostylis* as having a crown of rounded appendages at the apex. He also described the flowers of *Rhynchophora* as bisexual and those of *Calyptostylis* as unisexual. I now have flowering and fruiting material of a species that I believe probably represents *Calyptostylis*. Its fruit is fundamentally similar to that illustrated for *Rhynchophora humbertii* by Arènes, and its flowers are staminate on some plants and morphologically bisexual on others. I therefore see no basis for maintaining two genera for these species, and have selected *Rhynchophora* to be the correct name when they are combined. See the description and discussion of *Rhynchophora phillipsonii* below.

In his 1946 discussion, Arènes suggested that *Rhynchophora* is probably closest to another genus endemic to Madagascar, *Microsteira* Baker. I agree; in fact, the genera are so similar that I can distinguish them only on the basis of their ovaries and fruits. The fruit of *Microsteira* breaks apart at maturity into three samaras, each with a small dorsal crest and a three-lobed Y-shaped lateral wing; the similarity to the samara of *Triopterys* L. is striking. One can recognize the initials for the crest and lateral wings on the ovary even in flower. In *Rhynchophora* the three or four carpels are firmly connate and apparently never separate. At maturity each carpel bears a single elliptical wing that is neither dorsal nor lateral, but at right angles to the dorsiventral plane of the carpel. The result is a three- or four-winged fruit that resembles a helicopter with its wings raised ca. 45°. Arènes suggested that the single wing represents the lower lobe of the three-lobed wing of *Microsteira*, but if so it must have shifted its position from the base of the fruit to the middle or apex. Another possibility is that it is derived from the lateral wings of that samara, but it is so strange that the homology is not obvious and only comparative developmental study is likely to settle the matter. *Rhynchophora* deserves its generic status on the strength of its unique fruit, but given the otherwise strong similarity between it and *Microsteira*, I do not think the difference in their fruits justifies recognizing the tribe Rhynchophoreae Arènes, Notul. Syst. (Paris) 12: 135. 1946, unless one enlarges it to include the sister genus *Microsteira*.

Rhynchophora phillipsonii W. R. Anderson, sp. nov.—TYPE: MADAGASCAR. Toliara: 38 km SW of Ampanihy, on road to Androka, calcareous plateau, 200 m, 24°50'S, 44°25'E, 5 Feb 1990 fl/fr, *P. B. Phillipson, J.-N. Labat, D. & B. Du Puy 3451* (holotype: MICH!; isotypes: MO! K!). Fig. 1.

Liana gracilis; lamina foliorum majorum 3.5–6.3 cm longa, 1–3.3 cm lata, anguste elliptica vel anguste ovata vel ovata, adaxialiter mox glabrata, abaxialiter pertinaciter tomentosa vel laxe sericea, petiolo 5–14 mm longo, stipulis interpetiolaribus, 0.7–5.5 mm longis, saepe deciduis; flores staminati vel bisexuales, in plantis separatis portati (species ut videtur androdioecia); calyx eglandulosus; petala alba, ungue ca. 1 mm longo, limbo 4–5 mm longo, 3–3.5 mm lato; flores staminati 10–12 staminibus instructi, sine gynoecio; flores bisexuales 10 staminibus instructi et ovario 3–4-carpellato, stylis 3–4, stigmate terminali, magno, adaxialiter inciso; fructus siccus, indehiscens, sericeus, nuce 8–9 mm longa, cylindrica sulcataque, apice 3–4-alatus alis 12–15 mm longis, 5–7.5 mm latis, ellipticis vel obovatis.

Slender woody vine; stems initially golden-sericeous, the hairs fading to white and then deciduous, the older stems glabrate, red to brown. Leaves opposite; lamina of larger leaves 3.5–6.3 cm long, 1–3.3 cm wide, narrowly elliptical or narrowly ovate to ovate, cuneate, truncate, or rounded at base, mostly acute (sometimes slightly obtuse) at apex, initially appressed-puberulent above but soon glabrate, persistently tomentose or loosely sericeous below with the hairs raised, ± sinuous, white on the lamina, yellow fading to white on the midrib, eglandular or bearing 1 button-shaped gland on margin near base on one or both sides or rarely on abaxial surface of lamina slightly above base, with 5–7 pairs of principal lateral veins, the veins and reticulum prominent below, obscure above; petiole 5–14 mm long, loosely sericeous or tomentose to belatedly glabrescent, mostly eglandular but rarely with 1–2 small glands near apex; stipules 0.7–5.5 mm long, subulate, sericeous except for glabrous apex, borne on stem adjacent to leaf bases, often deciduous. Inflorescence loosely sericeous, paniculate with the flowers borne ultimately in short-stalked umbels or condensed corymbs of 4–13 or more; bracts 0.8–1.5 mm long, subulate or very narrowly triangular, abaxially sericeous, adaxially glabrous, eglandular, ± persistent; peduncle 0.5–2 mm long; bracteoles like bracts but only 0.3–0.6 mm long, borne at or slightly below apex of peduncle; pedicel 5.5–9 mm long. Flowers apparently radially symmetrical, staminate or morphologically bisexual with the two types borne on different plants. Sepals 5, alike, 1.5–1.8 mm long, 0.8–1 mm wide, distinct, ovate or elliptical, obtuse or rounded at apex, eglandular, abaxially densely sericeous, adaxially glabrous, appressed in anthesis. Petals 5, white, glabrous or with a few straight appressed hairs abaxially in center, spreading in anthesis, the claw ca. 1 mm long, the limb 4–5 mm long, 3–3.5 mm wide, flat or concave, ovate or broadly elliptical, entire or somewhat erose or denticulate. Stamens 10–12 in staminate flowers, 10 in "bisexual" flowers, glabrous, ± alike; filaments filiform, straight, short-connate only at very base, ca. 2 mm long in "bisexual" flowers (not fully elongated?), 3.5–4.5 mm long in staminate

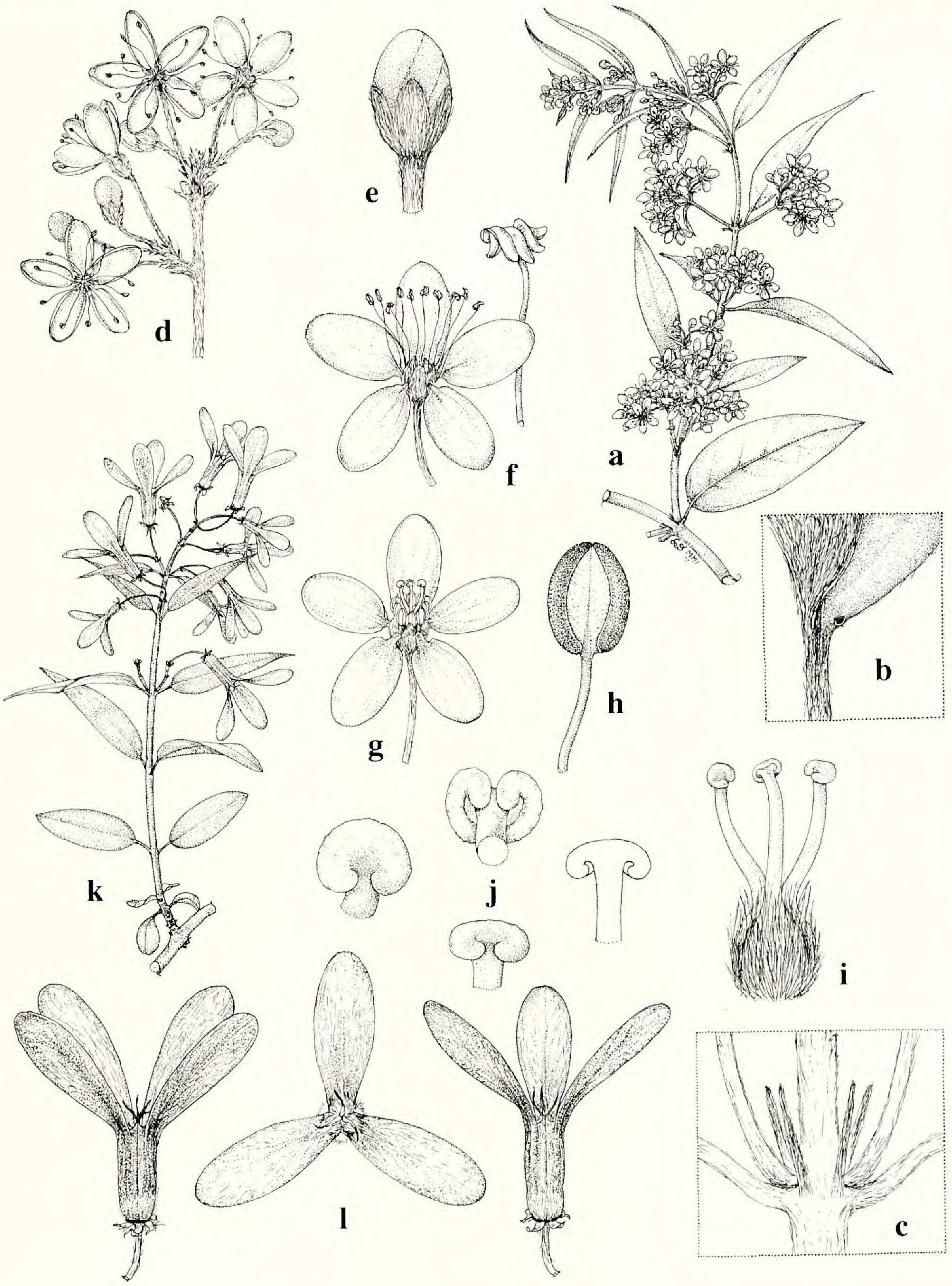

FIG. 1. *Rhynchophora phillipsonii.* a. Branch with staminate flowers, ×0.5. b. Base of lamina with marginal gland, ×5. c. Node with stipules, ×2.5. d. Cluster of staminate flowers, ×1.5. e. Bud of staminate flower, ×5. f. Staminate flower, ×2.5, and old stamen with twisted anther, ×15. g. "Bisexual" flower, ×2.5. h. Young anther from "bisexual" flower, ×15. i. Gynoecium, ×10. j. Style tips, three external views and one longitudinal section, ×30. k. Branch with fruits, ×0.5. l. Fruits, two side views and one from above, ×1.5. C. C. Davis has pointed out that in this species the flowers actually stand with two petals up and one down, rather than one up and two down as shown above. Drawn by Karin Douthit. (Based on: a–f, *Phillipson et al. 3424*; g–l, *Phillipson et al. 3451*.)

flowers; anthers 0.7–1 mm long, opening longitudinally, basifixed, the locules separated on a wide flat connective, becoming twisted in age. Staminate flowers without any rudiment of a gynoecium; gynoecium of "bisexual" flowers 3- or 4-carpellate; ovary ca. 1.3 mm long, cylindrical, densely sericeous, with as many locules as carpels, each locule containing 1 ovule; styles as many as carpels, ca. 2–2.2 mm long (not fully elongated?), slender but of uniform thickness their whole length, straight or slightly arcuate-ascending, the stigma terminal, large, reniform in outline but incised to style on adaxial side, revolute at margin, stigmatic over the whole upper surface. Fruit 3- or 4-carpellate, dry, indehiscent, samaroid, consisting of a cylindrical nut bearing wings at its apex, 1 wing per carpel; nut 8–9 mm long, 3–4 mm in diameter, deeply sulcate between carpels, each carpel with a raised abaxial midrib and very prominent reticulum on sides, densely sericeous; wings 12–15 mm long, 5–7.5 mm wide, elliptical or obovate, rounded at apex, sericeous on both sides and veiny with the veins prominent on both sides, departing from very apex of carpel and raised at an angle of ca. 45° from the horizontal, the plane of the wing perpendicular to the dorsiventral plane of the carpel, each style persistent at base of corresponding wing; seeds not seen.

ADDITIONAL SPECIMENS EXAMINED: **Madagascar**. TOLIARA: N of Toliara, in Forêt de Mikea, 23–25 road-km W of Vorehe, deciduous forest on sand, 50 m, 22°15'S, 43°25'E, Feb yg bud, *McPherson 17383* (MICH) & Feb stam fl, *McPherson 17397* (MICH); 16 km N of Ejeda on Route National 10, 300 m, 24°17'S, 44°29'E, Feb stam fl, *Phillipson 3424 et al.* (K, MO).

The epithet of this species honors Peter B. Phillipson (b. 1957), the South African botanist who collected the type and one of the paratypes.

As noted above, it is quite possible that this species is the same as *Calyptostylis humbertii* Arènes, Notul. Syst. (Paris) 12: 131. 1946, which was described from the same region. I have not seen the type, *Humbert 14358*, and it was so young that the nature of its fruit can only be surmised. In any case, Arènes's name in *Calyptostylis* cannot be used in *Rhynchophora*, because *R. humbertii* is preoccupied; *Rhynchophora humbertii* Arènes is the type of the genus. I have seen no specimens of *R. humbertii*, but Arènes's illustration of its fruit (Notul. Syst. [Paris] 12: 128. 1946) shows the wings attached at or below the middle of the nut, with a long conical projection of the nut above the wings; that difference alone establishes that these are different species. Moreover, Arènes described the petals of *R. humbertii* as 3 mm long and 2 mm wide, with a claw only 0.2 mm long; the petals of *R. phillipsonii* are larger.

The individuals of *Rhynchophora phillipsonii* bear either wholly staminate flowers or apparently bisexual flowers, i.e., the species is morphologically androdioecious, which is a very rare breeding system in flowering plants (G. Anderson & Symon 1989). One therefore wonders whether the pollen in the anthers of the "bisexual" flowers is functional. Unfortunately, the limited material available to me makes a proper study of the pollen in this species impossible at this time. However, I was able to make a superficial comparison of the two pollen types, which I mounted in lactophenol-cotton blue and examined with a light microscope. Both kinds of grains took up the cotton blue, indicating that they both contain cytoplasm, and both are spherical, but otherwise they are significantly different. The pollen from staminate flowers is thick-walled (and correspondingly slow to take up the stain). It lacks ectoapertures, but has (5) 6 (7) non-equatorial pores. The pollen from the morphologically bisexual flowers has walls that are about half as thick, and it takes up the stain much faster. Its diameter is about

20% greater (meaning its volume is about 80% greater). Most importantly, it is (as far as I can tell with the light microscope) completely inaperturate. From these observations I conclude that this species is functionally dioecious, not androdioecious, and the pollen of the "bisexual" flowers serves only as fodder, i.e., as the reward for the pollinators. This pattern is similar to that described by G. Anderson & Symon in *Solanum* (1989). The flowers in *Rhynchophora* bear no calyx glands and (like other Malpighiaceae) have no other kinds of nectaries associated with the flowers, so that (as in the species of *Solanum* discussed by Anderson & Symon) the only obvious reward for pollinators is pollen. If the pollinators visit only flowers that reward them with some kind of pollen, one would expect that the pistillate flowers in a dioecious species would be constrained by selection to retain either anthers with fodder pollen or anther-mimics that can fool the pollinators into visiting the pistillate flowers often enough to effect pollination. In this case the former seems to be the solution adopted. This hypothesis should be tested through careful study of the pollen when ample material is available. Eventually someone with access to living specimens should determine whether the putatively nonfunctional pollen will germinate *in vitro* and on stigmas, and if so, whether it can fertilize the ovules and produce viable seeds. Only one specimen of *Microsteira* with young "bisexual" flowers is available to me, but in that (*McPherson 14360*, MO) the anthers bear large inaperturate pollen grains like those described above for *Rhynchophora phillipsonii*, which suggests that this functional dioecy evolved in the common ancestor of the two genera and any study of the breeding system of *Rhynchophora* should also include *Microsteira*.

The fruit of *Rhynchophora phillipsonii* has the carpels connate only along a narrow central axis of tissue, but in the material available to me they can be separated only by force, for which reason it seems likely that the fruit is dispersed as a single unit. The wall of each carpel has longitudinal corky swellings along the midrib and sides where the dorsal and lateral wings would develop in other genera. The plane of the single wing suggests possible homology with the lateral wings of *Microsteira*, but the wing is never notched and its venation is not double, so there is no evidence that it is derived from displacement upward and fusion of two lateral wings. Given the disposition of wings on the fruit (see Fig. 1), it seems likely that successful dispersal of *R. phillipsonii* requires the fruit's indehiscence, which is almost certainly a derived condition (related genera mostly have the carpels separating at maturity; see Fig. 7 in Davis et al., in press). In the only fruiting collection available to me (*Phillipson et al. 3451*), the seeds are immature, although the fruits appear to be fully formed. Cross-sectioning of a number of those fruits showed that all the locules are well developed and most contain enlarging seeds, which suggests that the fruits are regularly dispersed with three or four seeds together. Such a method of dispersal would not be unique in the Malpighiaceae (see below), but it is certainly unusual in the family and, I suspect, in seed plants in general. One would expect the irrevocable dispersal of several sibling seeds together to be disadvantageous, because only one of them would be able to survive, even if more than one were to germinate. Most multiseeded fruits have evolved mechanisms by which the seeds separate either before or during dispersal, e.g., the seeds of animal-dispersed fruits often separate when voided. Indehiscent fruits have evolved several times in the Malpighiaceae (see Fig. 7 in Davis et al., in press). In *Bunchosia* the seeds surely separate when they are voided, and the same may be true of *Malpighia* (Davis et al., in press). In *Burdachia, Dicella, Glandonia*, and *Mcvaughia* the fruit is usually one-seeded through abortion of all but one ovule (W. Anderson 1979, 2001), which avoids the inefficiency of dispersing several seeds together. However, the byrsonimoid clade (*Blepharandra, Byrsonima,* and *Diacidia*; see Davis et al., in press, Figs. 5 and 7) produces two or three seeds in a completely indehiscent stone, such that they are most unlikely ever to separate (W. Anderson 2001). My observations of *Caucanthus auriculata* (Radlk.) Nied. and *Tricomaria usillo* Hook. & Arn. suggest that they, like *Rhynchophora*, disperse several seeds together in an indehiscent fruit. Of all the cases cited, the byrsonimoid fruit is the least likely ever to dehisce; there is a possibility that the fruits of *Caucanthus, Rhynchophora,* and *Tricomaria* actually do break apart belatedly. If not, there would seem to be an evolutionary anomaly in these several malpighiaceous clades that would repay further investigation.

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